

THE DISTRIBUTION OF PIGMENT AND OTHER MORPHOLOGICAL CONCOMITANTS OF THE METABOLIC GRADIENT IN OLIGOCHÆTS

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INTRODUCTION

The form of the antero-posterior metabolic gradient of the Oligochaets has now been well established by many workers and by almost as many different methods. Hyman (1916) investigated the gradient of susceptibility to KCN in many lower Oligochaets and distinguished two types, a primary gradient found only in the primitive *Æolosomatidæ* and young zoöids of the *Naididæ* in which the susceptibility decreased progressively from head to tail, and a widely distributed secondary type in which the susceptibility again rose at the posterior end. In *Lumbriculus varians* measurements of the oxygen intake of different regions of the body by the Winkler technique (Hyman and Galigher, 1921) showed a secondary metabolic gradient; the accurate manometric determinations of Shearer (1924) on the "earthworm" confirm the primary but throw no light on the secondary gradient, since the experiments were only made on head and tail portions. The early work of Morgan and Dimon (1904) on the potential gradient showed that in *Lumbricus terrestris* and *Allolobophora fatida* the head and tail were electronegative to the middle region, while Moore and Kellogg (1914) found that in an electric field *Lumbricus* oriented itself in the form of a U with head and tail towards the cathode. Hyman and Bellamy (1922) confirmed these results and correlated them with the metabolic gradient. Hatai (1924) showed that in two Japanese species of *Pheretima* (incorrectly named *Perichæta*) the amount of heat required to produce initial heat rigor in the muscles of the body wall was greatest at the anterior and posterior ends and least in the middle region of the body. He correlated these results with the percentage water content of the body wall, which is inversely proportional to the temperature required to produce initial heat rigor. Watanabe (1928) found that in *P. communissima* the potential gradient is on the average of the secondary type, although dorsally it is perhaps of the primary type.

Recently Perkins (1929) has published a short note in which he

claims that in earthworms the gradient of extractable reduced sulphydryl reaches a maximum in the mid anterior region of the body. Perkins summarizes his results as follows, "In earthworms I find that the gradient of growth corresponds with the gradients of total iodine equivalence, extractable sulphydryl, and total sulphur (gravimetric) and not with the gradient of total metabolism observed by the oxygen uptake; the last, therefore, includes other oxidation systems which it is legitimate to suppose result in katabolism rather than the anabolism of growth. It is interesting to find that gradients in the earthworm have a summit at about that point whence a divided worm grows forwards or backwards according to the aspect of the cut surface."¹

As regards the dorso-ventral gradient very little work has been done, although Hatai (1924) states that the temperature necessary to produce initial heat rigor is greater for dorsal than for ventral and intermediate for lateral portions of the body wall.

Little attention has been paid to the morphological concomitants of the metabolic gradient. Hess (1924) showed that the sensitivity of *Lumbricus terrestris* to light is greatest at the anterior end and least in the mid region of the body and that except on the first five and last two segments it is confined to the dorso-lateral regions; he also noticed that the distribution of pigment corresponds rather closely to the light sensitivity. In a later paper Hess (1925) showed that the distribution of the photo-receptor organs coincides with the distribution of the photo-sensitive regions, thus putting the gradient of sensitivity to light on a morphological basis. Nomura (1926) has extended the work of Hess, showing that in the ventral nerve cord of *Allolobophora fætida* Sav. there is an axially graded distribution of photic response; negative orientation, which also characterizes the brain, increasing posteriorly and positive orientation anteriorly, while the supposed neurones causing backward crawling are apparently restricted to the anterior end opposing the brain, which controls forward crawling.

DISTRIBUTION OF PIGMENT

Many species of earthworm are pallid and others may be colored green, blackish, or yellow by as yet uninvestigated pigments, but by far the most commonly occurring coloration is due to a reddish or purplish-brown pigment which has been shown in some species (see Kobayashi, 1928) to be a porphyrin allied to some derived from chlorophyll. This reddish pigment is characteristically distributed on the dorsal side and is most intense at the anterior end. A typical case can be found in the well-known species *Lumbricus terrestris* Linn. Indi-

¹ References to text figure omitted.

viduals of this species will be found to vary somewhat in the intensity and exact extent of pigmentation, but the following description taken from a specimen recently caught near this laboratory will serve as an example: "Intensely pigmented dorsally at the anterior end, the pigmentation extending laterally to about *cd* (the line of the lateral setæ), the first three segments also slightly pigmented ventrally; posterior to the clitellum the lateral extent of the dorsal pigmentation becomes reduced until only a mid-dorsal line is left which persists throughout the posterior half of the body; at the extreme posterior end there is again an increase in intensity and extent of pigmentation (except on the terminal segment which is small and pale) which extends laterally to below the setal line *cd* on the seventh to the second last segments and even faintly on the ventral side of the second, third, and fourth segments from the end." In this case the distribution of pigment follows the secondary type of gradient, and it may be said in general that whenever a species of earthworm exhibits this red-brown pigmentation (presumed, but of course not proved in most genera to be due to a porphyrin allied to that of *Lumbricus* and *Allolobophora* (*Eiscnia*) *fatida* Sav., it will be distributed according to the primary if not the secondary type of gradient. Hatai (1924) noticed that in "*Perichæta*" *megascolidioides* Goto et Hatai the dorsal side was more pigmented than the ventral, though curiously enough he did not correlate this with the dorso-ventral gradient. My own investigations have so far been confined to a systematic examination of South African species of the genera *Chilota* and *Acanthodrilus*. In these genera every gradation from total pallor to intense pigmentation can be found; some of the most interesting cases are those species, or varieties of otherwise pallid or pigmented species, in which pigmentation is only found on the first or last few segments. For example, the Cape Flats species *Acanthodrilus arundinis* Bedd. is pigmented dorsally on the first and last four or five segments but more intensely on the latter, while in many undescribed species of *Chilota* only a few of the anterior segments are pigmented. When the dorsal pigmentation is intense and occurs along the whole length of the body it is usual to find that the first five to ten segments are deeply pigmented ventrally, while in many cases pigment is deposited on the thickened septæ and generally on the inner side of the body wall at the anterior end. A more complete discussion will be given in my forthcoming paper on the South African Acanthodrilinæ.

The distribution of pigment in Oligochæts may be compared with that described by Faris (1924) for *Amblystoma* embryos. In this case the pigment is apparently a melanin and is deposited in regions of tissue differentiation as opposed to regions of proliferation. If the intensity

of pigmentation in Oligochaets is really a function of the metabolic rate, it seems possible that highly pigmented species would have a higher oxygen intake than pallid ones. It is hoped to investigate this point shortly on a large number of species. If this view is correct, and it is supported by the fact that pallid species are more sluggish in their movements and less irritable to handling than pigmented ones (compare *Allolobophora* (*Eisenia*) *rosca* Sav. with species of *Lumbricus*), it would seem unlikely that the porphyrin is merely derived from the food of the worm, as has been suggested, and more probable that it is a breakdown product of the worm's own hæmoglobin.

MULTIPLICATION AND REDUCTION OF SETÆ

As regards the more specifically morphological concomitants of the axial gradient, certain stages in the reduction and multiplication of setal numbers are significant. In the primitive lumbricine condition there are two pairs of setæ per segment except on the first, which never has setæ; a reduction in numbers sometimes takes place as in species of the *Microchaetus benhami* group where setæ are absent on the first six or seven segments of the adult (frequently only the lateral pair are absent on segment 6). This trend to reduction finds an extreme case in *Tritogonia crassa* Mchlsn., in which only the ventral setæ of the clitellar region persist.

In the Enchytræidæ parallel cases can be found; in the genus *Distichopus* only ventral setæ are present. In the genus *Michaelsena* transitional species occur from *M. mangeri* Mchlsn., in which dorsal and ventral setæ are present throughout and *M. principissæ* Mchlsn., in which the ventral setæ commence on segment 3 and the dorsal on segment 14, to *M. normani* Mchlsn., which has ventral setæ from segment 3 onwards but dorsal setæ only on segments 4-6, and *M. subtilis* Ude., in which dorsal setæ are absent and ventral setæ occur only on segments 4-6. In the genus *Achæta* setæ are totally absent. These cases may be compared with the phenomenon of cephalization in the Naididæ (Stephenson, 1912 and 1923), in which certain anterior segments are devoid of dorsal (*i.e.* lateral) setæ. Hyman (1916) found a very peculiar gradient in the Naid *Chaetogaster diaphanus*, in which the susceptibility was least at the head end. In this genus dorsal setæ are totally absent and ventral setæ though present on segment 2 are absent on segments 3, 4, and 5.

The tendency to setal multiplication is a very widely distributed phenomenon, and the perichæatine condition has apparently arisen independently many times in various families of the terrestrial or Neo-Oligochaets (see Stephenson 1921, 1923 for a discussion of this and

other trends in the evolution of the Indian Oligochaeta). The multiplication of setae varies from a condition in which six or eight pairs occur instead of four per segment to the purely perichæatine condition in which each segment has a complete ring, but the most interesting cases are those in which a transitional condition exists. In *Megascolex willeyi* Mehlsn. there are eight setae per segment at the anterior end and twelve in the middle and posterior regions; in *M. vilpattiensis* Mehlsn. there are eight setae in four pairs on segments 2 and 3, eight or nine on segment 4, *circa* 11 on segment 13, *circa* 24 on segment 26, and *circa* 26 at the posterior end. In general in transitional species the smaller number and 1 or more primitive paired condition persist at the anterior end. Sufficient data are unfortunately not available as to the extreme posterior end, so that it is not possible to state whether the smaller number also persists there in these intermediate forms. Hatai (1924) has investigated the setal numbers in the purely perichæatine species "*Perichæta*" (*Pheretima*) *megascolidioides* Goto et Hatai. He finds that the number of segments is extremely constant and bears no relation to the size of the worm and that the total number of setae per worm does not vary very greatly. The number of setae per segment increases from segment 2-25, remains about constant up to segment 100 and then decreases again, thus exhibiting a curve comparable with the secondary type of oligochaet gradient. From a survey of the available data it would thus seem as if setal multiplication were correlated with a lower and setal reduction with a higher metabolic rate. The case of *Acanthobdella peledina* Grube, an aberrant parasitic form regarded until recently as a leech, must not be overlooked, although the evidence (c.f. *Chatogaster*) cannot be interpreted until the form of the metabolic gradient has been investigated. In this species setae are present only ventrally on the first five segments.

MULTIPLICATION AND REDUCTION OF NEPHRIDIA

The trend to setal multiplication is paralleled and usually accompanied by the multiplication of the nephridia, primitively one pair per segment. Unfortunately the whole subject of nephridial multiplication stands in need of a thorough revision since the publication of Bahl's admirable series of studies on *Pheretima* (1919 and 1922), *Lampito* (1924) and *Hoodwardia* (1926). The brief descriptions of systematists who classified their species as "micronephridial," "meganephridial," and "mixed mega-and-micronephridial" are now shown to be totally inadequate. Nevertheless, what little can be judged from the existing knowledge yields points of considerable interest. In the first place, loss or reduction of nephridia when it occurs seems to take

place at the anterior end, *e.g.* in *Pontodrilus*, *Sparganophilus* and *Diporochæta pellucida* Bourne (*re* last species see Stephenson, 1925). Bahl considers that the first step in nephridial multiplication was the separation of the nephrostome, which then either disappeared or formed with accompanying nephridial cells a separate septal meganephridium opening into the gut, while the main mass of the nephridium broke up to form funnel-less integumentary nephridia. In *Pheretima* the septal nephridia have also undergone multiplication to the micronephridial condition. If this view be provisionally accepted, the two trends, separation of the nephrostome and multiplication, may be considered independently. As regards the former, numerous cases can be found in the literature in which "meganephridia" occur only in the middle and posterior regions of the body. In "*Lampito*" (*Megascolex*) *trilobata* Steph. and "*L.*" *mauritii* Kinb., Bahl found that the septal meganephridia commenced in segment 19, while in *Woodwardia bahli* Steph. they commence at 24/25. Benham (1905) describes two species of *Spenceriella*,—" *Diporochæta*" *gigantea* and "*D.*" *shakespearei*, which are "micronephric" but retain large paired nephrostomes in each segment. Unfortunately he does not say how far forward these occurred. In *Comarodrilus graveleyi* Steph. "micronephridia" occur in the anterior part of the body as far back as segment 12; behind this "meganephridia" only. In the development of *Octochætus multiporus*, Beddard found (1892) that the nephrostomes degenerate after their separation from the nephridial mass, but that they may persist in the posterior segments. These cases appear to be merely examples of a very general phenomenon, *viz.*, the tendency for the nephrostomes to disappear anteriorly. An interesting case is that of *Howascolex corethrurus* Mehlsn., a species which is transitional both for perichæatine and micronephridial conditions. The setæ are lumbricine in the anterior and middle regions and perichæatine posteriorly, while "meganephridia" displace the "micronephridia" posteriorly.

The case of nephridial multiplication *sensu stricto* requires a statistical investigation, but observations such as those of Bahl on "*Lampito*" and *Pheretima* spp. and of Stephenson on *Hoplochatella kinneari* Steph. indicate that a great multiplication in numbers of micronephridia in the clitellar region may be a general phenomenon.

While there is thus considerable evidence that nephridial and nephrostomal reduction follows the primary metabolic gradient, occurring first at the anterior end, the case of nephridial multiplication is not at all clear cut and the issue is frequently confused by the occurrence of pharyngeal nephridia (tufts of funnel-less nephridia opening into the pharynx) in the most anterior segments. The clitellar region, which

is sometimes the region of greatest multiplication (*vide supra*), is not known to be the region of lowest metabolism, since the physiological gradient has not been investigated for the species concerned, but evidence from other species suggests that the clitellar region is too far forward to coincide with the region of lowest metabolism. If Perkins' (1929) speculations as to the anabolic gradient are well founded, it is possible that certain morphological features such as nephridial multiplication in the clitellar region might be interpreted more readily by a correlation with this rather than with the total metabolic gradient. Examples have been cited above in which "micronephridia" are replaced by or co-exist with "meganephridia" in the posterior part of the body. Sometimes, *e.g.*, in *Notoscolex palniensis* Steph., these "meganephridia" are definitely stated to be enlarged "micronephridia" without funnels (Stephenson, 1924). Cases of nephridial multiplication without separation of the nephrostome are extremely rare. Bahl (1926) has described the case of "*Lampito*" *dubius* Steph., and apparently a similar phenomenon occurs in the genus *Tritogenia*, which has two pairs of nephridia per segment. In "*Lampito*" *dubius* there are five pairs of septal exonephridia per segment except anteriorly, where there may be only three pairs. On the whole there is a suggestion that nephridial multiplication is less pronounced in the regions of highest metabolism.

HOMŒOSIS

Finally, I should like to draw the attention of zoölogists who have not made a study of oligochaet systematics to the very general occurrence of homœosis, not merely as occasional variations (Bateson, 1894) but as normal subspecific, specific, generic and family characters, the segmental shifting forwards and backwards of various organs, *e.g.* the clitellum, genital openings, and accessory glands, gizzard, etc. being of prime taxonomic importance. An excellent example may be taken from the genus *Acanthodrilus*, which normally possesses paired male pores on segment 18 and two pairs of prostatic pores on segments 17 and 19; there may, however, be a backward shifting (Michaelsen, 1913) as in *Ac. conceensis* Mehlsn. and *Ac. natalicius* Mehlsn. with the male pores on segment 19 and prostatic pores on 18 and 20 or *Ac. rouxi* Mehlsn. with the male pores on segment 20 and the prostatic pores on 19 and 21. A similar phenomenon occurs in undescribed South African species of *Chilota*.

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SUMMARY

In Oligochaeta the distribution of the photoreceptor organs and of porphyrin pigmentation as well as the tendencies to reduction and multiplication in numbers of setae and of nephridia per segment appear as morphological concomitants of the metabolic gradient.

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